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MAMMALIAN FOSSILS OF SAMOS AND PIKERMI. PART 2. RESURRECTION OF A CLASSIC TUROLIAN FAUNA

Nikos Solounias[1]

Abstract

A brief history of the known Pikermi and Samos paleontological expeditions is presented. The quarries of Samos have been relocated. The interrelationship of local stratigraphy at Samos, radiometric samples, and quarries enabled the inference that all the bone horizons are essentially of one age (8.5–9 *Ma*). Bones accumulated primarily in overbank and paleosol deposits, they show little transport and are frequently concentrated in lenses. Bones probably accumulated either in local depressions and/or due to droughts. Although the Pikermi and Samos localities have been explored since the 1830s, this is the first modern revision and reevaluation of the entire fauna; many unreported taxa are added to the species lists. Pikermi and Samos sample species of one or two fairly similar faunas. The differences between Pikermi and Samos are at least due to sampling bias, time, and ecology. Samos represents the more diverse sample of the fauna and perhaps slightly more open country conditions.

Introduction and History of Excavations

The Late Miocene (Turolian) localities from Samos Island and Pikermi, Greece, are significant because of their key location between Europe, Asia, and Africa, the quantity of fossils, their quality of preservation, the brevity of space and geologic time represented, and especially the diversity of species. There is no other late Miocene locality in Eurasia or Africa that records, in such a narrow stratigraphic interval, as many mammalian species as Samos. A study of Samos and

[1] Address: Divison of Vertebrate Paleontology, Peabody Museum of Natural History, Yale University, New Haven, CT 06511.

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Table 1.—*Museums housing Pikermi and Samos fossils.*

AMNH	—American Museum of Natural History, New York	(P), S
BM(NH)	—British Museum of Natural History, London	P, S
CM	—Carnegie Museum of Natural History, Pittsburgh	P, S
GPIT	—Geologisches und Paläontologisches Institute und Sammlungen, Tübingen	S
HLMD	—Hessischer Landesmuseum, Darmstadt	P, S
MGL	—Musée Géologique, Lausanne	S
MGPUP	—Musea Geologia-Paleontologia dell Università di Padova	P, S
MHNG	—Musée d'Histoire Naturelle Genève	(P), S
MHNL	—Musée d'Histoire Naturelle, Lyon	P
MHNP	—Musée National d'Histoire Naturelle, Paris	P, (S)
MNKF	—Freiburg (Brisgaw) Museum für Naturkunde	S
MPM	—Mytilinii Paleontological Museum, Samos	S
NHMBa	—Naturhistorisches Museum Basel	(P), S
NHMBe	—Naturhistorisches Museum, Bern	S
NHMW	—Naturhistorisches Staatsmuseum, Wien	P, S
NMB	—Naturhistorisches Museum, Berlin	P, (S)
NNLH	—Naturkundeabteilung des Niedersächischen Landesmuseum, Hannover	S
PIA	—Paleontological Institut, Athens	P, (S)
PIM	—Mineralogisches und Geologisches-Paläontologishes Institute, Münster	S
PIUW	—Paläontologishes Institute Universität, Wien	P, S
RMS	—Naturhistoriska Riksmuseum, Stockholm	P
RPMH	—Roemer-Pelizaeus Museum, Hildesheim	S
SMF	—Senckenbergische Naturforschende Gesellschaft, Naturhistorisches Museum, Frankfurt	S
SMNL	—Staatl Museum für Naturkunke, Ludwigsburg	S
SPGM	—Sammlung für Paläontologie und Historische Geologie, München	P, S
UCM	—University of Colorado Museum, Boulder	S
UGR	—Ungarn Geological Institute, Budapest	S
USNM	—National Museum of Natural History, Washington	(P), (S)
YPM	—Yale Peabody Museum, New Haven	(P)
ZMH	—Zoologisches Museum, Hamburg	S

P = Pikermi, S = Samos, ( ) means only few specimens.

Pikermi provides valuable evidence in solving biostratigraphic, biochronologic, and paleontological problems. Samos and the faunally similar but less species-rich Pikermi are two classic mammalian localities explored primarily during the nineteenth and early twentieth centuries. This brief study presents the first detailed stratigraphy and the first complete faunal reevaluation and revision since Forsyth Major's 1894 study.

Pikermi, 21 km northeast of Athens, was discovered by the English archeologist Georges Finlay, who excavated with Anton Lindermayer

Table 2.—*History of known paleontological excavations at Pikermi.*

Date	Collector	Exact region	Approximate number of specimens	Museum
1835	Finlay, Lindermayer	Unknown	Unknown	PIA, Athens
1838	Bavarian soldier rediscovers Pikermi			
1839–1850	Wagner	Unknown	300 500 traded to other museums or destroyed in World War II	SPGM, Munich
1853	Mitsopoulos	Unknown	Unknown	PIA, Athens
1853	Minister Baron, Fourth Rouen	Unknown	Unknown	MHNP, Paris
1854	Dr. Chaeretis	Unknown	30	MHNP, Paris
1855–1856, 1860	Gaudry	Unknown	1,000	MHNP, Paris
1860–1870	Unknown	Unknown	60	RMS, Stockholm
1882	Dames	Unknown	Unknown	NMB, E. Berlin
1885	Newmayr and Tausch	Unknown	300	PIUW, Vienna
1901	Woodward	Unknown	2,500	BM(NH), London
1910–1920*	Skoufos	Unknown	Unknown	PIA, Athens
1912–1922	Abel	Unknown	3,500	PIUW, NHMW, Vienna
1970–1974	Symeonidis, Zapfe, de Bruijn, and others	Chomateri locality	100	PIA, Athens

* Approximate.

Table 3.—*History of the known paleontological excavations at Samos.*

Date of collection	Collector	District	Approximate number of specimens	Museum
Before 1852	Italian travellers	Unknown	25	MGPUP, Padova
1887	C. I. F. Major	Andrianos, Stefana, Potamies	1,600 30 10	MGL, Lausanne MHNG, Geneva NHMBa, Basel
1889	C. I. F. Major	Stefana,* Vrysoula*	500	BM(NH), London
1893	G. Bukowski	Unknown	20	PIUW, Vienna
1889–1900	K. von dem Borne commissioned by Sturtz in Bonn	Andrianos, Potamies Vrysoula, probably others	2,100	SMNL, Ludwigsburg; SPGM, Munich; MHNP, Paris; NHMW, Vienna; BM(NH), London; probably HLMD, Darmstadt; NNLH, Hanover; MNKF, Freiburg; GPIT, Tübingen
1897	T. Stützel	4 unknown localities	100 (many destroyed in W.W. II)	SPGM, Munich**
1901–1902	A. Hentschel	Same 4 unknown localities as Stützel	100	SPGM, Munich**
1901	E. Fraas	Unknown	25	SPGM, Munich; SMNL, Ludwigsburg
1909–1920	K. Acker	All localities	2,500	NHMW, Vienna; SMF, Frankfurt, SMNL, Ludwigsburg; ZMH, Hamburg; RPMH, Hildesheim; NHMBe, Bern; NHMBa, Basel

Table 3.—*Continued.*

Date of collection	Collector	District	Approximate number of specimens	Museum
1909	T. Werner	Potamies and other localities	2,000	PIM, Münster
1911	T. Kormos	Unknown	Unknown	UGR, Budapest
1912	D. Psilovikos	Unknown	100	AMNH, New York***
1913	G. J. Weinberger	Unknown	20	NHMW, Vienna
1921–1924	B. Brown	Tholorema, Limitzis, Andrianos, Potamies, Megalos Vrahos, Vrysoula	3,000	AMNH, New York
1939*	Germans	Potamies	Unknown	Unknown
1963	J. Melentis	Andrianos	50	MPM, Mytilinii
1976	N. Solounias	Andrianos, Potamies	150	UCM, Boulder

* Uncertain.
** 51 specimens from Munich were sold to CM, Pittsburgh, by Schlosser.
*** Brown purchased these specimens for the AMNH.

in 1835. Three years later a Bavarian soldier of the Greek King Othon discovered a monkey skull filled with calcite crystals which he mistook for diamonds. It was his arrest in Munich for grave robbery that initiated the first extensive excavations by Andreas Wagner conducted from 1839 to 1850. Following Wagner, Albert Gaudry excavated in 1855–1856 and 1860, and studied the entire Pikermi fauna. In 1885, Melchor Neumayr and L. v. Tausch excavated for the PIUW, Vienna (see Table 1 for museum names). Arthur Smith Woodward collected for the BM(NH), London, in 1901; and finally, the last major excavation was made by Othenio Abel for the PIUW and NHMW, Vienna, between 1912 and 1922. At least six more minor excavations have been conducted at Pikermi by Swedes, Germans, Italians, Greeks, and others. In addition, museum trading has distributed the fossils of Pikermi throughout the world (Table 1). Table 2 briefly summarizes the traceable Pikermi excavations.

The Samos fossils, unlike those of Pikermi, were known to ancient Greeks. They were rediscovered by Italian travellers who took a small collection to the University of Padova between 1852 and 1866. The first excavations brought to scientific attention were conducted by Charles Immanual Forsyth Major in 1887 and 1889. He was also the only worker who studied the entire Samos fauna. Following Major's work, the beds (Table 3) were repeatedly excavated by several German parties and, later, by Barnum Brown (1921–1924) for the AMNH, New York (Table 4).

Primarily, most of the Samos and Pikermi collections were made to enrich museums rather than to collect the fossils for systematic research. In general, more paleontologists worked at Pikermi than at Samos which was excavated almost exclusively by museum personnel and businessmen (Solounias, 1979; 1981). The significance of the Samos fauna was not apparent, because the fossils were dispersed to so many museums. Samos may also have been overlooked because it was similar to Pikermi and because it could have been considered an isolated island fauna.

Because workers neglected to reveal the specific locations of their excavations, the exact position of the Pikermi bone beds is not accurately known. For example, despite Gaudry's 1862–1867 detailed Pikermi monograph, no locality map was included. A similar problem existed at Samos. Forsyth Major reported the general location of his 1887 quarries (Solounias, 1979; 1981). With the help of Dimetrios Psilovikos, who worked for the earlier German parties, Brown discovered all the sites excavated prior to 1921. The Samos bone beds were located by using old museum labels indicating geographic landmarks, old photographs, letters, notes, careful mapping of bone fragments in the field, and interviewing old farmers who worked for Barnum Brown.

Table 4.—*Information on the Samos bone beds.*

Bone bed	District	Land owner	Excavated by**	Date
Q6	Tholorema	Wasteland	Brown	1921–1924
L	Limitzis	Emmanuel Nikolaou Leondidis, 1915	Acker	1909–1920
Q5	Limitzis	Soumas, 1924–1978 (east of Papamoschatos' farm in 1978)	Brown	1921–1924
A	Andrianos	Aristarchos Sofoulis, 1924	Major Acker	1887 1909–1920
Q1	Andrianos	Aristarchos Sofoulis, 1924	Brown Melentis Solunias	1921–1924 1963 1976
Q2	Potamies	Efstathios Validakis, 1924; George Papaemmanuel, 1980	?Werner Brown	1909 1921–1924
Q4	Potamies	Trifon Validakis, 1924; Christos Validakis, 1980	Brown	1921–1924
S2	Potamies	Efstathios Validakis, 1924; George Papaemmanuel, 1980	Solounias	1976, 1979
S3	Potamies	George Papaemmanuel, 1980	Solounias	1976, 1979
S4	Potamies	Wasteland	Solounias	1976
Q3	Megalos Vrahos	Gliarmis, 1924; Lefteris Efthimiou, 1980	Brown	1921–1924
S	Stefana	Unknown	Major	1887, 1889*
G	Smakia	Kostas Konstantinidis, 1890; Stefanos Papaioannou, 1980; next to land of Kostas Fregadiotis, 1980	German collectors	
QX	Vrysoula in Mytilinii	Army base	?Major Brown	1889* 1921–1924
AG	Agiadhes	Unknown	No one	

* Date uncertain.

** These excavators are definitely known, but most sites were probably prospected and/or excavated by others. This is especially true for bone beds L, A, and Q2.

LOCAL STRATIGRAPHY AND AGE

The local stratigraphy of the Pikermi horizons has not been studied thoroughly. Previous work on the geology has been general (Gaudry 1862–1867; Lepsius, 1893; Abel, 1927) as has been the recent research (von Freyberg, 1951; Symeonidis et al., 1973; Symeonidis and Marcopoulou-Diacantoni, 1977). The sediments cannot be radiometrically dated.

The five to seven bone beds of Pikermi occur in a 0.5 by 3.0 km area along the Megalo Remma ravine. They are confined to no more than 50 m of section and thus are not greatly different in age from each other. Although no formation has been formally recognized (I propose the use of Pikermi Formation as in Abel, 1927:83) for the bone bearing deposits, and although there is no information as to the exact locality of each fossiliferous horizon, the following lithologies occur at Megalo Remma ravine: (a) massive reddish mudstones, 60 to 150 cm thick; (b) dark maroon, laterally discontinuous mudstones no more than 3 to 15 cm thick; (c) lenticular conglomerates, 20 cm to 6 m thick, of well rounded gravels. Some of these conglomerates are as much as 100 m broad and 6 meters deep in cross section; generally most are 3 to 15 m broad and 60–120 cm thick. The clasts are well sorted marbles and originated from the surrounding basement; (d) massive algal limestones.

Recent geologic research at Samos has revealed a tectonically complex basin with many lithologies (Van Couvering and Miller, 1971; Meissner, 1976*a*, 1976*b*; Angelier, 1976; Solounias, 1979).

The 15 bone beds of Samos are confined to the Mytilini Formation with the exception of three minor fossiliferous horizons, and span no more than 100 m of section and occur within only 5 km of each other[1] (Figs. 1, 2, and 3) (Solounias, 1979). These fossiliferous horizons contain abundant tuffs which allow K-Ar dating analyses. Recent research by Marc Weidmann and myself on the stratigraphy suggests that the Mytilini Formation may represent no more than 0.5 *Ma* of deposition (Fig. 2). According to the available K-Ar dates, the age of these bone beds is approximately 8.5 *Ma*. Thus their age is exclusively Turolian unlike other reports (Van Couvering and Miller, 1971; Berggren and Van Couvering, 1974; Mein, 1975). More detailed research on age determination and stratigraphy is in progress (Curtis, Drake, Solounias, and Weidmann).

Within the Mytilini Formation most of the bone occurs in the Main Bone Bed member except for two minor accumulations (Figs. 1, 2 and 3). The Main Bone Beds include the following lithologies: (a) poorly sorted volcanicalistic marls and mudstones, 50 to 150 cm thick; (b) marls and mudstones differing from (a) in being better sorted, unstratified and without major pebble and gravel horizons; (c) bedded clay nodule horizons which occur within (a) and (b). Most of the nodules are composed of the same material as the surrounding matrix; some encase pebbles or bone. These horizons are one nodule thick, approximately 3 to 10 cm, and are not laterally continuous for more than 6 to 8 m; (d) well defined lenticular gravel and pebble conglomerates, 40

[1] L, Q5, Q1, Q2, Q3, S2, S3, S4 and Q4 only 1.2 km by .5 area (see Fig. 1).

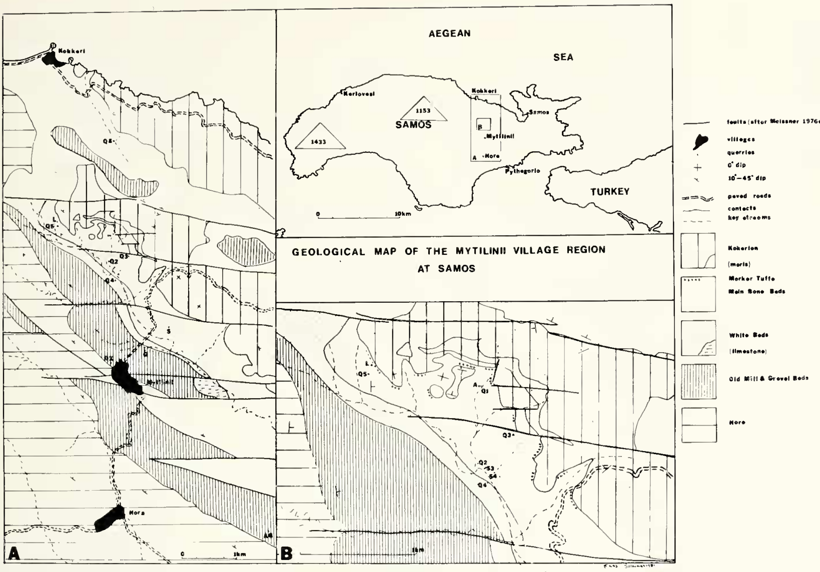

Fig. 1.—Geological map of the Mytilinii Village Region at Samos.

to 350 cm thick. They are often deep and narrow but can also be shallow and broad. The clasts are poorly sorted, angular limestone or marble, and originated from formations older than the Mytilini Formation; (e) water-lain pumice tuffs, 50 to 150 cm thick, which change laterally into other lithologies. Most of the tuffs fine upward. Their lower contact is often transitional but the upper is abrupt.

The Bone Beds

I define a bone bed as follows: a region where bones from various animals are densely concentrated and surrounded by regions where bones are absent or not concentrated.

The taphonomy of Samos and Pikermi has not been studied, and taphonomic information is limited because most of the fossils have already been excavated. However, a few observations can be made from unprepared museum blocks from Samos and Pikermi, from field study of old quarries on Samos only, from bone beds still containing fossils on Samos only, and from the tens of thousands of bones from Samos and Pikermi which are now in museums.

At both sites bone forms lenses. Only rarely can isolated fossils be found, but this might be due to the absence of flat exposures where more of the bedding planes can be observed. Some of the bone beds were 30 by 15 m in area and about 25 to 60 cm thick. Others were only 3 by 10 m in

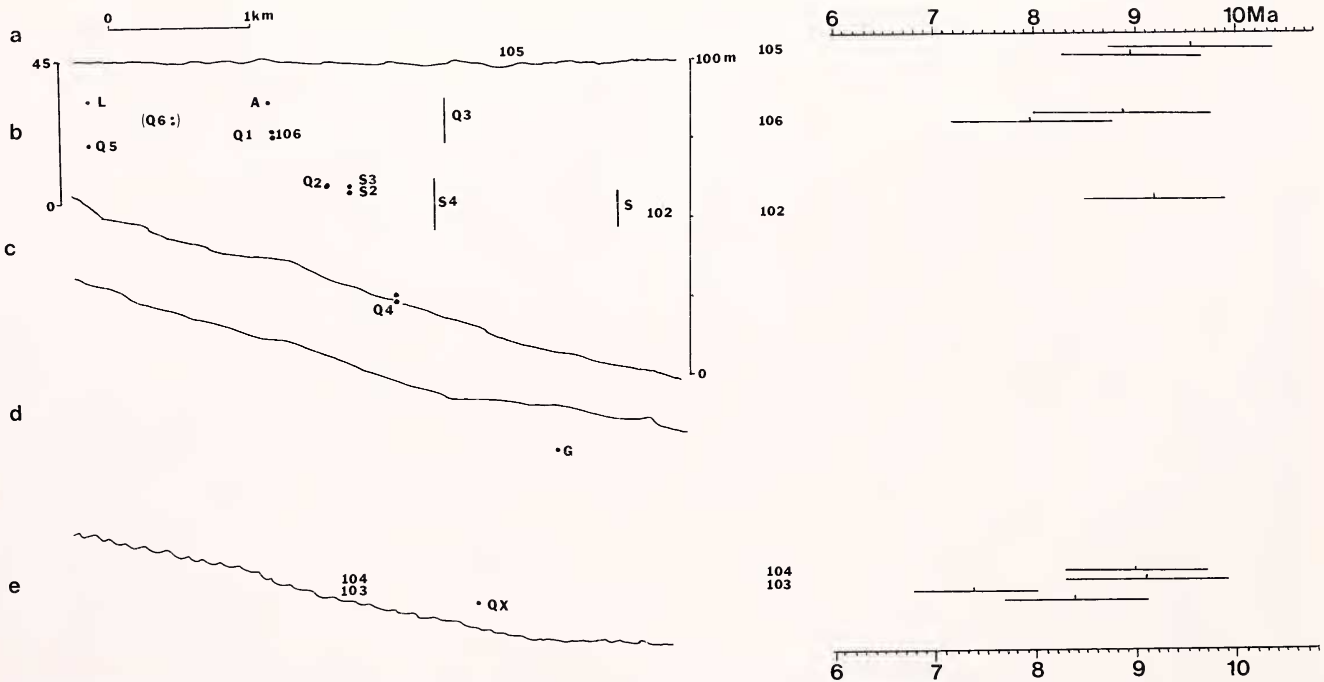

Fig. 2.—Stratigraphic distribution of the K-Ar samples and the bone beds. A dot indicates the exact position of a particular bone bed. Two dots indicate two-layered bone beds. A line indicates that the exact stratigraphic position is known only within the limits of the line. A good estimate for the Samos fauna is 8.5–9 *Ma*. Bone bed abbreviations as in Table 4. 102, 103, 104, 105 and 106 are radiometric sample numbers of Van Couvering and Miller, 1971. a, Marker Tuffs; b, Main Bone Beds; c, White Beds; d, Old Mill Beds and Gravel Beds; e, Hora Formation.

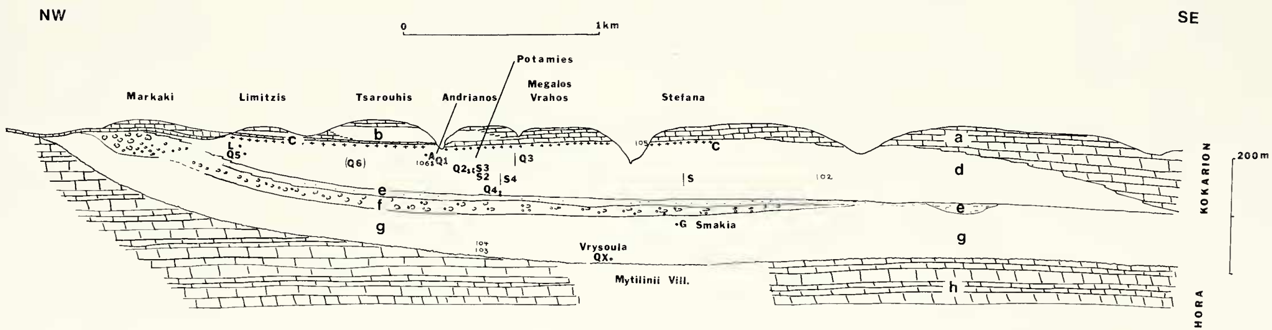

Fig. 3.—Schematic NW-SE cross section of the Mytilinii Valley showing the position of the bone beds. Abbreviations as in Fig. 2 and Table 4. Q6 is projected in the valley. 102, 103, 104, 105, 106 are radiometric sample numbers of Van Couvering and Miller, 1971. a, Kokarion (limestones); b, Kokarion (marls); c, Marker Tuffs; d, Main Bone Beds; e, White Beds; f, Gravel Beds; g, Old Mill Beds; h, Hora. In a different direction the extent of the lithologies is different.

area and 25 cm thick. In quarries, bone was often discontinuous in distribution. In most cases, bone was densely packed with no particular orientation; skulls, jaws, limbs, and horns of all sizes were mixed. Remains of proboscideans, small to large carnivores and antelopes, rodents and bats were found next to each other. At both there is a notable absence of aquatic elements, such as invertebrates, fish, water turtles, and crocodiles. At both, most of the taxa are ungulates. Rodents, small mammals, carnivores, and primates are not as represented as in other synchronous localities.

Few of the bones from Samos and Pikermi are weathered; they show little transport as the complex surfaces of skulls, teeth, and bones are often unbroken and unabraded. Isolated teeth and abraded bone are rare. Many broken surfaces are clearly due to poor excavation techniques while others are due to weathering before fossilization. In artiodactyls, skeletal parts not commonly preserved are premaxillae, anterior dentitions and symphyses, tips of horns, mandibular ascending rami and angles. Complete long bones and their distal and proximal ends are common. Hands and feet are often articulated. Juvenile epiphyses are not commonly preserved.

At Pikermi most of the bones and skulls are flattened and crushed. Many bones were found either as parts of articulated skeletons (especially the extremeties) or as isolated skulls, skull fragments, and limb fragments. Isolated bovid horn cores and frontlets were also common. Jaws are rarely associated with skulls.

In comparison, at Samos much less bone is flattened. There are fewer partially articulated skeletons and also unlike Pikermi, there is a more pronounced absence from Samos of ribs, scapulae, pelves, and axial vertebrae of larger mammals and the absence of axial bones and limbs of smaller mammals.[1] It is this absence of axial elements that makes the abundance of skulls, jaws, and limbs so noticeable. Bovid horn cores and frontlets are common, but again the jaws are usually not associated with the skulls. Unlike those of Pikermi, about one third of the bones of Samos are coated with a crust of marly limestone.

At Samos, bone is not associated with the channel deposits, but occurs mainly within the fine marls and the clay nodule horizons.

INTERPRETATION

The preliminary depositional interpretation for Pikermi is as follows: lithology (a) represents overbank flood plain deposits; (b) paleosols; (c) channel deposits of well developed, mature streams not particularly near the source; (d) freshwater lakes.

[1] April 4, 1924, Brown's letter to Osborn: ". . . there are many perfect horse skulls and sufficient limb bones for a restoration, but I am still short of vertebrae and ribs . . . ."

The preliminary depositional interpretation for Samos is as follows: lithologies (a) and (b) represent overbank deposits; (c) paleosols or sheet flow deposits; (d) channel deposits of small streams near the source; (e) overbank deposits. The source of the ash is not known. The clastics come from the basement and from formations older than the Mytilini.

Presently Pikermi and Samos can be considered relatively instantaneous samples of late Miocene biotas when compared with longer time sequences such as Maragheh, the Chinji, or the Shan Si deposits (Van Couvering, Raza, and Tedford, personal communication).

Interpreting the origin of bone beds is not simple. There are no data on recent bone beds similar to those of Samos and Pikermi. The Samos bone beds are probably the result of a number of processes that have occurred between the living community and the final deposition of bones including an unknown accumulation time. As for the last step in this long chain of bone deposition events, I propose two plausible explanations knowing that they are merely speculative and certainly not sufficient. One is that some bone beds could be the result of sheet wash. Another is that they could be depression accumulations.

Behrensymeyer (personal communication) has observed that during floods, sheet wash may occur. Sheet wash is flood water flowing with such speed that it does not fill depressions and channels but flows over the higher areas. (1) This flow could accumulate bones from a floodplain surface. (2) While bones in depressions of a floodplain would be protected from such flow, bones at higher topographic regions would be carried away.

Bones are in general well preserved. A plausible explanation for this would be minimal transport, although cadavers can sometimes be transported with no apparent damage to the bones and teeth. Bones are also closely packed together in piles with no consistent orientation. Topographic depressions would favor this type of accumulation.

Additional evidence for a depression hypothesis comes from the bone beds and the local stratigraphy. At least three of the largest bone beds, Brown's Quarries 1, 2, and 4 were two superimposed layers of bone.[1] The same was true for S-3 and S-2 which were separated by 1

[1] December 4, 1923. Letter to Matthew from Barnum Brown about his Q1. ". . . Specimens so far seen in this quarry are a wash accumulation. Only a few bones such as feet are associated, and many have been rotted or broken before fossilization. There are two bone strata over part of the quarry, separated by one and a half feet of earth, the lowermost carrying the best material was deposited in turgid water with thin fine grained clay seams overlying bones, while the upper strata has pebbles and large stones intermingled with the bones. It seems to be of common occurrence in the Mytilinos area to find two bone layers close together, one underlying the other . . ." American Museum of Natural History Archives. Also personal field observation of bone fragment distribution suggests that Quarries 2 and 4 were two layers.

m of tuffaceous marl. If bones were accumulating in depressions for some time, they would permit other layers of bone to form in superposition (Behrensmeyer, personal communication). At Quarries 1 and 2 and the S-3 and S-2 sites the lower layer of bone was less extensive than the upper. This observation also suggests the presence of depressions. Concave regions would tend to contain less bone in their lower part.

Preliminary work on the sediments suggests the existence of larger local depressions. Several lithologic members of the Mytilini thin out and do not occur except at the bone bed region. Laterally neither these members nor bones were ever found. These are the Gravel Beds, the White Beds, the Marker Tuffs, the unrounded conglomerates of the Main Bone Beds, and finally thick marl beds which occur within the Kokarion Formation only in the vicinity of the bone beds (Fig. 3). Depressed areas probably favored the formation of these local deposits and the better preservation of bone. It is important to note here that the depressions favoring the accumulation of bone would be between 8 to 30 square m. The depressions favoring the deposition of the previously mentioned lithologic members would be between 3 to 6 square km. Hence there may not be a close relationship between the two.

Criteria for distinguishing catastrophic from attritional mortality in fossil samples by means of age-frequency distributions have been proposed by Voorhies (1969: plate 13). Attritional mortality in fossil mammal samples results in the accumulation of primarily the young and old, because they have higher mortality rates than the adults. Catastrophic mortality results in a census of the living population; age distributions for medium-sized mammals tend to be dominated by adults. Hence catastrophic death samples, being relatively instantaneous events, resemble theoretical age distributions (for example Pianka, 1978; fig. 5-3; Ricklefs, 1973: fig. 34-1 through 4).

Although neither the fossil population from Samos nor Pikermi has yet been studied in detail, preliminary work indicates that most individuals are adults, suggesting that some of the bone beds could be caused by catastrophic deaths. Abel (1922) suggested a catastrophic death at Pikermi. He hypothesized that brush fires drove the herds over cliffs. Ungulate tibiae (unreported number) in his collections displayed spiral fractures similar to those that occur in skiers. The tibiae display the V-shaped fracture pointing downward on the longer fractured portion (Abel, 1922, 1927: fig. 138). In his reconstruction ungulates falling over the cliffs would break their legs, but primates and carnivores could climb down (Abel, 1927: fig. 139). Abel's samples were unavailable for study but many collections from Pikermi do not show such fractures.

Other reasons for bone accumulations have been suggested. For example Gaudry (1854; 1867), Lepsius (1893), and Schlosser (1904:115) have proposed that bone beds are the result of flood accumulations. Lepsius (1893) also suggested the possibility of carnivore den accumulations. Judith Van Couvering and I have noticed that the Turolian is characterized by rich bone beds throughout Eurasia while the Vallesian and other older stages have deposits where bone is frequently uniformly abundant (background bone) but not particularly concentrated into bone beds. The marked faunal change during the Turolian might be the result of more seasonal climates implying that during droughts more animals would die. Hence, Vallesian, and especially pre-Vallesian stages, record less seasonal environments, Turolian and post-Turolian stages more seasonal ones with periodic droughts resulting in rich bone beds.

The depression and drought hypotheses for Pikermi and Samos are not necessarily mutually exclusive. Our research team is presently investigating these possibilities (Badgley, Behrensmeyer and Solounias, work in progress).

How much time does a single bone horizon represent? Recent bone accumulations need to be studied in order to answer this question. Some of the Samos bone beds could be either a day or hundreds of years old. Future research with recent bone depositions and the development of a nomenclature for different types of bone beds is needed in order to understand better the Pikermi, Samos, Maragheh, and Shan Si localities.

The absence of aquatic elements is significant and needs to be investigated further. Two tentative speculations are that no permanent water systems were developed in the vicinity of the bone beds and that the bones accumulated primarily on hard surfaces This is contrary to the assumed interfingering of the Kokarion Formation (freshwater lakes) (Fig. 3). Perhaps the Kokarion is significantly younger throughout and filled low areas to the southwest (Fig. 3). The absence of aquatic elements is in agreement with a drought hypothesis and the brief time of deposition.

Carnivore action is a plausible explanation for the absence of vertebrae, ribs, and the smaller limbs at Samos. Hence the Pikermi bones could have been buried relatively faster.

Crusts around the bones from Samos suggest the presence of some organic material during deposition, or of algal growth on the bones, or of a precipitate on the bones because they were in supersaturated standing water (Behrensmeyer, personal communication).

RECONSTRUCTION OF SPECIES LISTS

Most of the vertebrate familes represented at Pikermi and Samos have been systematically studied. A literature review is presented in

Table 5.—*Literature review.*

Most significant publications on the fauna as a whole
Wagner, 1847
Roth and Wagner, 1854
Gaudry, 1862–1867
Weithofer, 1888
Abel, 1922, 1927
Major, 1891*a,* 1894

Molluscs
de Stefani et al., 1891

Turtles
Szalai, 1933

Birds
Gaudry, 1862–1867

Insectivores
Rumke, 1976
Black et al., 1980

Chiroptera
Revilliod, 1922

Primates
Wagner, 1847
Roth and Wagner, 1854
Gaudry, 1862–1867
Delson, 1973

Rodents
Dames, 1883*a*
Schaub, 1926
Abu, 1959
Freudenthal, 1970
de Bruijn, 1976
Black et al., 1980

Lagomorphs
Martinez, 1976

Carnivores
Gaudry, 1861*a*
Gaudry, 1862–1867
Hensel, 1862
Major, 1902*a*
Schwarz, 1912
Dietrich, 1927
Pilgrim, 1931
Helbing, 1932
Pilgrim, 1933
Kurtén, 1954
Abu, 1959
Ficarelli and Torre, 1970
de Beaumont, 1961, 1964, 1967, 1968, 1969

Tubulidentates
Major, 1893
Andrews, 1896
Colbert, 1941

Proboscideans
Schlesinger, 1922
Lehmann, 1950

Hyracoids
Major, 1899*a,* 1899*b*
Schlosser, 1899
Osborn, 1899

Hipparions
Hensel, 1860
Kormos, 1911
Studer, 1911
Abel, 1926
Wehrli, 1941
Forstén, 1968, 1980
Sondaar, 1971
Woodburne and Bernor, 1980

Rhinocerotids
Weber, 1904, 1905
Andree, 1921
Heissig, 1975

Chalicotheres
Dietrich, 1928
Schaub, 1943
Schaffer and Zapfe, 1971
Symeonidis, 1973

Suids
Pilgrim, 1926
Thenius, 1950

Giraffids
Wagner, 1861
Gaudry, 1861*b,* 1861*c*
Major, 1891*b,* 1894, 1901, 1902*b,* 1902*c*
Black, 1915
Schlosser, 1921
Bohlin, 1926, 1935*a*
Colbert, 1938
Churcher, 1970
Hamilton, 1978

Bovids
Gaudry, 1861*c,* 1862–1867
Dames, 1883*b*

Table 5.—*Continued.*

de Beaumont and Mein, 1972	Major, 1894
Hunt, 1974	Schlosser, 1904
Schmidt-Kittler, 1976	Andree, 1926
Galiano and Frailey, 1977	Pilgrim and Hopwood, 1928
Hendey, 1978	Sickenberg, 1929, 1932, 1933
Howell and Petter, 1980	Bohlin, 1935*b*, 1935*c*
Kurtén, 1981	Sickenberg, 1936
	Gentry, 1970, 1971, 1974

Table 5. They all deal with selected specimens, selected species, and/or "wastebasket" species. Selected specimens and assignments to "expected" species have given a simplified picture of the number of taxa represented. A few studies have considered biological variation. Until this study the only comprehensive faunal studies were the originals—Gaudry's 1862–1867 for Pikermi and Major's 1894 for Samos. Consequently, the fauna had never been revised using modern systematics and all available specimens.

More than 30 natural history museums house the specimens. The examination of most specimens from a given locality is of utmost importance in reconstructing species lists because this method provides the only reference for overlooked and unreported species. It is not unusual for new genera, families, and even orders to be added to the fauna. Table 6 lists the new species whose paleogeographic range has been extended now to Pikermi and Samos. It is interesting to note that all these new taxa are rare and are represented by no more than one to five specimens, indicating that all the collected specimens should be examined in order to obtain the most comprehensive species lists. Constructing comprehensive species lists should be brought to the attention of researchers (1) comparing localities of heterogeneous geographic and stratigraphic magnitudes and of varying collecting time; (2) scientists who are recently excavating localities and are reporting species lists after few seasons of collecting; (3) scientists using poorly known localities for biochronology and biostratigraphy. The recognition of unreported taxa is strengthened when specimens are not assigned to "expected species" without examination.

SYSTEMATIC REVISION

Systematic revisions are often elaborate because they involve the comparison of species from a number of localities. Since many of the Pikermi and Samos taxa were originally described from these localities, revisions have been possible. The present revision (Table 7) was

Table 6.—*New occurrences of fossil animals at Pikermi and Samos.*

Specimen	Number (where known)	Pikermi	Samos
Rumina decolata			x
Parmacella sp.			x
Hellicella sp.			x
?Hymenoptera gen. and sp. indet.			x
Testudo cf. *marmorum*			x
Testudo schafferi	1–5	x	
Testudo sp. (very large)	1		x
Varanus marathonensis	1		x
Struthio caratheodoris	1	x	
Grus pentelici	1–5		x
Galerix atticus	3		x
Spermophilinus cf. *bredai*	1		x
Occitanomys? provocator	2		x
Pliospalax cf. *sotirisi*	3		x
Pseudomeriones pythagorasi	7		x
Ursavus cf. *depereti*	2		x
Parataxidea maraghana	1		x
Ictitherium viverrinum	2–5		x
Hyaena sp.	1		x
Thalassictis hyaenoides	3	x	
Thalassictis (*Lycyaena*) sp. nov.	1		x
Hyaeninae gen. and sp. indet.	2		x
Felis sp.	1	x	
Metailurus parvulus	1		x
Metailurus major	1		x
Mammut borsoni	1		x
Hipparion sp. small		x	x
Hipparion sp. large			x
Hipparion matthewi	1	x	
Sus sp.	1	x	
Dorcatherium naui	1		x
Muntiacus sp.	3–5		x
Cervidae gen. and sp. indet. (large)	1	x	
Pliocervus pentelici	1		x
?*Helladotherium* sp.	1		x
Samotherium sp.			x
Palaeotragus sp.			x
Miotragocerus valenciennesi	1		x
Samokeros minotaurus	1–5		x
Prosinotragus sp. nov.	1		x
Selenoportax sp. nov. indet.	1	x	
Rupicaprini gen. and sp.	3		x

accomplished over a 6-year period with the kind help of several specialists although the degree to which I have allowed myself to be influenced by their advice is my responsibility. I have also used my own knowledge of the hyaenids, equids, rhinocerotids, giraffids, and bo-

Table 7.—*Taxonomical revision of traditional nomenclature for the Pikermi and Samos species.*

Original taxa	Revised taxa
Carnivora	
Melodon maraghanus	*Parataxidea maraghana*
Promephitis majori	*Promephitis lartetii*
Ictitherium robustum	*Ictitherium viverrinum*
Palhyaena hipparionum	*Thalassictis wongii*
Palhyaena hipparionum (in part)	*Thalassictis hyaenoides*
Hyaena sp.	*Hyaeninae* gen. and sp. indet.
Lycyaena chaeretis (in part)	*Thalassictis* (*Lycyaena*) *chaeretis*
Lycyaena chaeretis (in part)	*Thalassictis* (*Lycyaena*) sp. nov.
Proboscidea	
Tetralophodon longirostris	*Stegotetrabelodon grandincisivus*
Zygolophodon turicensis or (?*Mastodon*) *tapiroides*	*Mammut borsoni*
Perissodactyla	
Hipparion mediterraneum	*Hipparion* sp. large
Hipparion cf. *proboscideum*	*Hipparion* sp. large
Hipparion matthewi (in part)	*Hipparion* sp. small
Stephanorhinus pachygnathus	*Dicerorhinus schleiermacheri*
Diceros neumayeri	*Diceros pachygnathus*
Artiodactyla	
Microstonyx erymanthius	*Sus major*
Palaeotragus quadricornis	*Palaeotragus coelophrys*
Palaeotragus rouenii (in part)	*Palaeotragus* sp.
Samotherium boissieri (in part)	*Samotherium* sp.
Bohlinia or *Giraffa speciosa*	*Honanotherium speciosum*
Bohlinia or *Giraffa attica*	*Honanotherium atticum*
Miotragocerus amalthea (in part)	*Miotragocerus monacensis*
Miotragocerus amalthea (in part)	*Tragoportax amalthea*
Miotragocerus rugosifrons (in part)	*Tragoportax curvicornis*
Miotragocerus rugosifrons (in part)	*Tragoportax rugosifrons*
Gazella pilgrimi (in part)	*Gazella capricornis*
Gazella pilgrimi (in part)	*Gazella dorcadoides*
Gazella deperdita (in part)	Rupicaprini gen. and sp. indet.
Ovis kuhlmanni	*Prosinotragus kuhlmanni*
Pachytragus crassicornis	*Protoryx crassicornis*
Pachytragus laticeps	*Protoryx laticeps*
Antilope of unknown genus	*Selenoportax* sp.
Samotragus crassicornis	*Sinotragus crassicornis*

vids. The revised species lists from Pikermi, Samos, and Maragheh, Iran, are shown in Table 8. There are 80 species at Pikermi and 100 at Samos. Maragheh is less species rich. The number of mammals is 68 at Pikermi and 86 at Samos. Pikermi and Samos share 45 common mammalian taxa. The number of species present at Pikermi and absent

Table 8.—*A cumulative species list for the localities at Pikermi and Samos, Greece, and Maragheh, Iran.*

Taxa	Pikermi	Samos	Maragheh
Mollusca			
Gastropoda			
Prosobranchia or Archaeogastropoda			
Rissoacea			
Hydropodidae			
Hydrobia cf. *ventricosa*	x	–	
Pulmonata or Stylommatophora			
Vertiginacea			
Enidae			
Buliminus samius	–	x	
Achatinacea			
Subulinidae			
Rumina decollata	–	x	
Zonitacea			
Limacidae			
Parmacella sp.	–	x	
Helicacae			
Pleurodontidae			
Hellicella sp.	–	x	
Helicidae			
Otala vermiculata	x	–	
Helix barbeyana var. *nasseana*	–	x	
Helix sprattiana	–	x	
Helix palaeocastrensis	–	x	
Arthropoda			
Insecta			
?Hymenoptera			
Gen. and sp. indet.	x	x	
Chordata			
Reptilia			
Chelonia			
Testudinidae			
Testudo cf. *marmorum* (small)	x	x	
Testudo schafferi (medium)	x	x	
Testudo sp. (very large)	–	x	
Squamata			
Varanidae			
Varanus marathonensis	x	x	
Aves			
Struthioformes			
Struthionidae			
Struthio caratheodoris	x	x	x
Ciconiiformes			
Ciconidae			
Ciconia sp.	x	–	
Galliformes			
Phasianidae			
Gallus aesculapii	x	–	
?*Phasianus archaiaci*	x	–	

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Ralliformes			
Gruidae			
Grus pentelici	x	x	
Ralliformes gen. and sp. indet.	x	–	
Urmiornis maraghanus	–	–	x
Eutheria			
Insectivora			
Talpidae			
Uropsilinae			
Desmanella dubia	x	–	
Erinaceidae			
Gymnurinae			
Galerix atticus	x	x	
Galerix moedlingensis	x	–	
Chiroptera			
Vespertilionidae			
Vespertilioninae			
Samonycteris majori	–	x	
Primates			
Cercopithecidae			
Colobinae			
Mesopithecus pentelici	x	–	x
Lagomorpha			
Ochotonidae			
Prolagus cf. *crusafonti*	x	–	
Leporidae			
Alilepus sp.	x	–	
Rodentia			
Sciuridae			
Spermophilinus cf. *bredai*	–	x	
Cricetidae			
Cricetinae			
Kowalskia cf. *lavocati*	x	–	
Cricetodontinae-Tribe Cricetodontini			
Byzantinia hellenicus	–	x	
Byzantinia pikermiensis	x	–	
Gerbillinae			
Pseudomeriones pythagorasi	–	x	
Muridae			
Murinae			
Parapodemus gaudryi	x	–	
Occitanomys ? neutrum	x	–	
Occitanomys ? provocator	x	x	
?*Gerboa* sp.	–	–	x
Spalacinae			
Pliospalax cf. *sotirisi*	–	x	
Gliridae			
Glirinae			
Muscardinus sp.	x	–	
Myomimus cf. *dehmi*	x	–	

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Hystricidae			
Hystricinae			
Hystrix primigenia	x	x	–
Carnivora			
Family indet.			
Simocyon primigenius	x	–	–
Ursidae			
Ursavus cf. *depereti*	–	x	–
Indarctos atticus	x	x	x
Mustelidae			
Mustelinae			
Sinictis pentelici	x	–	–
Martes sp.	–	–	x
Martes woodwardi	x	–	–
?*Plesiogulo* sp.	x	–	–
Melinae			
Promeles palaeattica	x	x	x
Parataxidea maraghana	–	x	x
Parataxidea polaki	–	–	x
Mephitinae			
Promephitis lartetii	x	x	–
Lutrinae			
?*Enhydriodon laticeps*	x	–	–
Hyaenidae			
Subfamily A			
Plioviverrops orbignyi	x	x	–
Subfamily B			
Thalassictis wongii	–	x	x
Thalassictis hyaenoides	x	–	–
Thalassictis (*Lycyaena*) *chaeretis*	x	x	–
Thalassictis (*Lycyaena*) sp. nov.	–	x	–
Subfamily C			
Ictitherium viverrinum	x	x	–
Hyaeninae			
Hyaena sp.	–	x	–
Gen. and sp. indet.	–	x	–
Subfamily D			
Hyaenictis graeca	x	–	–
Percrocuta eximia	x	x	x
Felidae			
Felinae			
Felis sp.	x	–	–
Felis attica	x	x	x
Subfamily indet.			
Metailurus parvulus	x	x	x
Metailurus major	x	x	–
Machairodontinae			
Machairodus giganteus	x	x	x
Paramachairodus orientalis	x	–	x
Tubulidentata			

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Orycteropodidae			
Orycteropus gaudryi	–	x	x
Proboscidea			
Palaeomastodontidae			
Mammut borsoni	x	x	–
Gomphotheriidae			
Gomphotheriinae			
Stegotetrabelodon grandincisivus	x	x	–
Choerolophodon pentelici	x	x	x
Dinotheriidae			
Deinotherium cf. *giganteum*	x	x	–
Hyracoidea			
Procaviidae			
Pliohyrax graecus	x	x	–
Pliohyrax kruppii	–	x	–
Perissodactyla			
Equidae			
Hipparion sp. (large, one preorbital fossa)	x	x	x
Hipparion sp. (small, one preorbital fossa)	?x	x	x
Hipparion proboscideum (large, two preorbital fossae)	–	x	–
Hipparion dietrichi (medium, no preorbital fossa)	–	x	x
Hipparion mattewi (small, no preorbital fossa)	x	x	–
Chalicotheriidae			
Chalicotherium goldfussi	x	–	–
Ancylotherium pentelicum	–	x	x
Rhinocerotidae			
Aceratheriinae-Tribe Aceratherini			
Aceratherium cf. *incisivum*	x	–	–
Chilotherium samium	–	x	–
Chilotherium schlosseri	–	x	–
Chilotherium kowalewski	–	x	–
Chilotherium persiae	–	–	x
Rhinocerotinae-Tribe Rhinocerotini			
Dicerorhinus schleiermacheri	x	x	–
Diceros pachygnathus	x	x	x
Rhinocerotinae-Tribe Elasmotherini			
Iranotherium morgani	–	–	x
Artiodactyla			
Suidae			
Sus sp.	x	–	–
Sus major	x	x	x
Potamochoerus hytheriordes	–	x	–
Tragulidae			
Dorcatherium naui	–	x	–
Cervidae			

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Muntiacinae			
Muntiacus sp.	–	x	–
Cervinae			
Cervinae gen. and sp. indet. large	x	–	–
Pliocervus pentelici	x	x	x
Giraffidae			
Palaeotraginae			
Palaeotragus rouenii	x	x	–
Palaeotragus sp.	–	x	–
Palaeotragus coelophrys	–	x	x
Samotherium boissieri	–	x	x
Samotherium sp.	–	x	–
Sivatheriinae			
Helladotherium duvernoyi	x	x	x
?*Helladotherium* sp.	–	x	–
?Giraffinae			
Honanotherium speciosum	x	x	–
Honanotherium atticum	x	–	x
Bovidae			
Miotragocerus-Tragoportax Complex			
Miotragocerus monacensis var. A	x	x	–
Miotragocerus monacensis var. B	x	x	x
Miotragocerus valenciennesi	x	x	–
Tragoportax amalthea	x	x	–
Tragoportax curvicornis	–	x	–
Tragoportax rugosifrons	?x	x	–
**Samokeros minotaurus* var. A	–	x	x
**Samokeros minotaurus* var. B	–	x	–
Tribe Antilopini			
Prostrepsiceros rotundicornis var. A	x	–	–
Prostrepsiceros rotundicornis var. B	–	x	x
Prostrepsiceros houtumschindleri var. A	–	x	–
Prostrepsicerus houtumschindleri var. B	–	–	x
Protragelaphus skouzesi	x	x	x
Gazella capricornis	x	x	–
Gazella mytilinii	–	x	–
Gazella dorcadoides	–	x	–
Gazella deperdita	–	–	x
Oioceros rothi	x	–	x
Oioceros atropatenes	–	–	x
Oioceros wegneri	–	x	–
?*Oioceros rodleri*	–	–	x
Sinotragus crassicornis	–	x	–
Sinotragus sp. nov.	–	–	x
Prosinotragus kuhlmanni	–	x	–
Prosinotragus sp. nov.	–	x	–
Tribe Ovibovini			
Palaeoreas lindermayeri	x	x	–
Criotherium argalioides	–	x	–

Table 8.—*Continued.*

Taxa	Pikermi	Samos	Maragheh
Parurmiatherium rugosifrons	–	x	–
Urmiatherium polaki	–	–	x
Protoryx Complex			
Palaeoryx pallasi	x	x	–
Palaeoryx sp.	–	x	–
Tragoreas oryxoides	–	x	–
Sporadotragus parvidens	x	x	–
Protoryx carolinae	x	–	–
Protoryx crassicornis (short-brained)	–	x	x
Protoryx laticeps (long-brained)	–	x	x
Protoryx laticeps (short-brained)	–	x	?x
Pseudotragus capricornis	–	x	–
Tribe Tragelaphini			
Selenoportax sp. nov.	x	–	–
Tribe Rupicaprini			
Gen. and sp. indet.	–	x	–

x Present. – Not present. An empty space means unverified absence due to lack of excavating for small animals.

* This is a new genus and species officially described in Solounias, 1981; see also Solounias, 1979.

from Samos is 35. Similarly there are 45 species at Samos which are absent from Pikermi.

SAMOS: STRATIGRAPHIC AND BIOSTRATIGRAPHIC COMPARISONS

Comparisons within bone horizons.—Most species occur together within a bone bed (Table 9). Specifically, Major's Andriano, quarry A, and Brown's Q1–6 and X show similarities in contained elements, species, and relative abundance (unpublished data).

Comparisons between bone horizons.—The stratigraphic location of some species may never be known because most Samos collectors did not keep field data (Table 3). Table 9 lists localities for species where known. These localities can be subdivided into stratigraphic levels (Table 9; Figs. 2 and 3) but again the species differences are minor and could be attributed to sampling bias. The major bone horizons at Samos are relatively the same age, 8.9–9.0 *Ma* (Figs. 2 and 3).

Many European collections with no stratigraphic data were almost certainly collected in the same locations where Brown's quarries were located (Figs. 1, 2, and 3). Brown, in a letter to Matthew, says that he had the same guide who had reputedly worked for the German parties. Brown reports that he reopened most of the German quarries because these were the only locations with bone at Samos. I also found bone

Table 9.—*Individual locality species lists for Samos. Non-included taxa have no stratigraphic information.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Buliminus samius									X							
Rumina decollata						X										
Parmacella sp.						X										
Hellicella sp.						X										
Helix barbeyana var. *nasseana*				X	X				X							
Helix palaeocastrensis					X											
?Hymenopera gen. and sp. indet.										X						
Testudo cf. *marmorum*									X							
Testudo schafferi						X										
Testudo sp. (very large)										X						
Varanus marathonensis						X				X						
Struthio caratheodoris									X							
Grus pentelici										X						
Galerix atticus						X										
Samonycteris majori									X							
Spermophilinus cf. *bredai*						X										
Pliospalax cf. *sotirisi*						X										
Byzantinia hellenicus						X			X							
Occitanomys? *provocator*						X										
Pseudomeriones pythagorasi						X			X							
Hystrix primigenia								X								X
Ursavus cf. *depereti*									X							
Promeles palaeattica									X	X						
Parataxidea maraghana									X	X						

Table 9.—*Continued.*

Taxa	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Thalassictis wongii		x				x		x	x	x					x	x
Thalassictis sp. nov.									x							
Promephitis larteti				x					x	x	x					
Plioviverrops orbignyi									x	x						
Ictitherium viverrinum									x	x						
Percrocuta eximia		x				x		x	x	x			x		x	x
Felis attica									x							
Metailurus parvulus								x	x							
Machairodus giganteus									x							
Orycteropus gaudryi									x						x	
Choerolophodon pentelici									x	x		x	x			
Mammut borsoni										x						
Deinotherium cf. *giganteum*									x							
Pliohyrax graecus												x				
Hipparion sp. large		x														
Hipparion sp. small							x		x							x
Hipparion matthewi								x	x					x		x
Hipparion proboscideum	x		x			x	x		x	x						x
Hipparion dietrichi						x	x		x	x						x
Ancylotherium pentelicum			x						x	x		x				x
Chilotherium samium		x	x	x			x		x	x		x				x
Chilotherium schlosseri														x	x	x
Chilotherium kowalewski																x
Dicerorhinus schleiermacheri			x					x	x	x		x		x		
Diceros pachygnathus		x	x					x	x	x		x	x		x	x
Sus major									x	x		x				x

Table 9.—*Continued.*

	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
Taxa	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Muntiacus sp.									X		X					X
Pliocervus pentelici									X							X
Palaeotragus rouenii			X						X	X			X			X
Palaeotragus sp.													X			
Palaeotragus coelophrys	X		X		X				X	X						X
Samotherium boissieri		X		X	X	X		X	X	X	X		X			X
Samotherium sp.										X						
Helladotherium duvernoyi									X	X						X
Honanotherium speciosum												X	X		X	
Miotragocerus monacensis				X						X						X
Miotragocerus valenciennesi								X								
Tragoportax amalthea			X	X					X	X	X			X		
Tragoportax curvicornis								X		X						X
Tragoportax rugosifrons		X						X	X	X				X		X
Samokeros minotaurus													X	X		X
Gazella capricornis	X					X		X	X	X	X		X		X	X
Gazella mytilinii								X	X						X	X
Gazella dorcadoides								X	X	X						X
Prostrepsiceros rotundicornis									X							
Prostrepsiceros houtumschindleri								X	X							
Protragelaphus skouzesi									X				X	X	X	
Oioceros wegneri									X							X
Prosinotragus kuhlmanni																X
Palaeoreas lindermayeri			X								X					
Criotherium argalioides				X					X	X	X		X			X

Table 9.—*Continued.*

Taxa	Bone beds of known stratigraphic position											Bone beds of unknown stratigraphic position				
	L1	L2	Level 3									Schlosser, 1904				Munster
	Qx	Q4	S	Q2	S2	S3	S4	Q5	A	Q1	Q6	1	2	3	4	PIM
Palaeoryx pallasi		X						X	X		X				X	X
Palaeoryx sp.									X							
Tragoreas oryxoides									X				X	X		X
Sporadotragus parvidens	X	X			X			X	X	X			X	X		X
Protoryx crassicornis					X			X						X		X
Protoryx laticeps		X	X		X		X		X	X				X		X
Pseudotragus capricornis					X				X		X	X				
Rupicaprini								X		X						

Within each level the bone beds are not listed in a stratigraphic order.

fragments only where quarries are reported to have been, confirming the existence of no more than 15 localities (Table 4).

Q1, A, Q2, S3, S2, S4, Q5, A6, S, and probably the PIM collection are stratigraphically close to one another; they could be as close as 30 m and no more than 60 m within the Main Bone Bed Member of the Mytilini Formation (Figs. 2 and 3) (Solounias, 1979; 1981). The degree of resolution is hindered by hundreds of small faults, plant cover, and absence of stratigraphic markers. The Marker Tuffs are above all bone beds and the White Beds below the Main Bone Bed Member (Figs. 2 and 3).

Mytilinii Village, Vrysoula district.—The oldest bone bed at Samos is QX. It is located 10 m above the Hora limestones and is within the Old Mill Beds Member of the Mytilini Formation (Figs. 2 and 3). The few specimens collected there by Brown show no differences from similar specimens of the Main Bone Bed Member. The BM(NH) 1889 Major collection could have come from QX. Again this collection shows no major faunal differences.

Smakia district.—At Smakia, G indicates the location of either all Munich collections or one of them. Schlosser (1904:112–115) reports fossils found in four distinct horizons. It is not certain whether they were all located together in superposition at Smakia or whether one of them was there and the others were perhaps at Potamies and/or Andrianos. The horizons at Smakia are presently covered with farms. The type of preservation of the Munich collection indicates that the fossils had been collected at Smakia only.

Stefana district.—Major's 1887 collection occurs at Stefana Hill and is at the same level as the Main Bone Beds.

Tholorema district.—Q6 is the most distant quarry. It contained two layers of bone like Q1, Q2, Q4, and S3–S2. The Q6 bones are few, they are fragmented and show indications of flood transport.

Andrianos district.—Major's quarry A is 9 m above Brown's Q1. There is a possibility that a fault may exist between the two that could make them the same level. Presently Brown's Q1 dump covers the area between Q1 and A. The Andrianos area is bound by faults.

Potamies district.—There is a syncline between Q1 and Andrianos and Q2 at Potamies which brings Q2 and Q1 stratigraphically close. The fault that separates Q1 from Q2 (Solounias, 1981: map 1) is in the middle of the syncline. The same fault disrupts the Kokarion limestones showing minor displacement. My micromammal locality S3 is horizontally 35 m from Q2. The type of preservation of Werner's 1909 collection at PIM is most similar to that of Q2 at the AMNH. It is possible that the PIM collection came from the Q2 or S3 region (Tables 3 and 4).

Limitzis district.—L is Acker's quarry and hence some of the Vienna, Ludwigsburg, and Frankfurt specimens could have come from there (Table 4). Q5 has been presented as a younger quarry (Sondaar, 1971; Gentry, 1971; Van Couvering and Miller, 1971; Mein, 1975). The reason was the presence of *Hipparion matthewi* and *Protoryx* (*Pachytragus*) *crassicornis* and the absence of *Hipparion proboscideum* and *Protoryx* (*Pachytragus*) *laticeps* at Q5. There are a few exposures between Q5 and Q1 but the Marker Tuffs are above Q5 and the White Beds below it as for all other quarries of the Main Bone Bed Member (Figs. 2 and 3). Thus Q5 is also part of the sequence. Q5 may even be slightly older than Q1, if actual sedimentary thicknesses are taken into consideration. *Protoryx* (*Pachytragus*) *crassicornis* is also found at S2 which is at the same level as Q2 and Q1. The type of *Protoryx* (*Pachytragus*) *crassicornis* comes from G which is older than Q1 (Figs. 2 and 3). In addition, specimens from A and PIM could be assigned to *Hipparion matthewi*.

PIKERMI VERSUS SAMOS: SPECIES COMPARISONS AND INTERPRETATION

In the future Pikermi and Samos will be compared to other fossil sites and with recent communities. The Aegean separates the two sites but is a relatively recent epicontinental sea and would not have been a barrier for late Miocene animals. The distance between Pikermi and Samos is 280 km. This distance is comparable with Siwalik localities (200 km), Shan Si localities (350 km) and no more than the Serengeti-Mara ecosystem (240 km).

There have been a number of attempts to compare Pikermi with Samos (Major, 1888, 1891*a*, 1891*c*, 1894; Abel, 1927; Pilgrim and Hopwood, 1928; Pilgrim 1931; Gentry, 1971; Van Couvering and Miller, 1971; Solounias, 1979, 1981, to name just a few). Most authors have correctly postulated that the differences are primarily the result of sampling, time, and ecology. The question, however, still remains unanswered: what is the relative importance of each? I treat each factor separately ignoring the others in order to simplify this discussion.

Differences attributable to sampling.—A similar number of specimens has been found at Pikermi and Samos.[1] Hence species comparisons ignoring relative numbers of specimens is possible.

[1] Unpublished data; approximately 50,000 specimens in each. This number may seem low when compared to other localities (Pilbeam et al., 1977). Absolute number of specimens can be misleading. For example, the Siwalik material is more fragmented than the Pikermi and Samos material. Also the size of the area prospected and the stratigraphic thickness sampled should be taken into consideration.

Table 10.—*Abundant and rare species at Pikermi and Samos.*

Shared abundant species (more than 30 specimens)	
Percrocuta eximia	*Palaeotragus rouenii*
Choerolophodon pentelici	*Gazella capricornis*
Diceros pachygnathus	*Palaeoryx pallasi*
Shared rare species (less than 30 specimens)	
?*Hymenoptera* gen. and sp. indet.	*Metailurus parvulus*
Testudo cf. *marmorum* (small)	*Metailurus major*
Testudo schafferi (medium)	*Machairodus giganteus*
Varanus marathonensis	*Mammut borsoni*
Struthio caratheodoris	*Stegotetrabelodon grandincisivus*
Grus pentelici	*Deinotherium* cf. *giganteum*
Galerix atticus	*Pliohyrax graecus*
Occitanomys ?provocator	*Hipparion* sp. (small, one preorbital fossa)
Hystrix primigenia	*Dicerorhinus schleiermacheri*
Indarctos atticus	*Pliocervus pentelici*
Promeles palaeattica	*Honanotherium speciosum*
Promephitis lartetii	*Honanotherium atticum*
Plioviverrops orbignyi	*Miotragocerus valenciennesi*
Thalassictis (*Lycyaena*) *chaeretis*	*Protragelaphus skouzesi*
Ictitherium viverrinum	
Felis attica	

In theory, sampling bias can never be excluded as the cause of the absence of a particular species, although for some species it is more unlikely than others.

In theory, the differences between Tables 8 and 10 as well as the abundance differences shown in Table 11 could be attributed to sampling bias. In this case Pikermi would be less different from Samos than Table 8 shows.

Time differences.—The similarity between the faunas (Tables 8, 10, and 11) suggest that the time differences are small. Pikermi cannot be dated radiometrically.

If Pikermi is older than Samos, perhaps late Vallesian or early Turolian (10.5–9.0 *Ma*), then the less diverse ungulates sampled at Pikermi would predate the radiation recorded at Samos (8.5 *Ma*). If Pikermi is younger than Samos, perhaps late Turolian or early Ruscinian (7.0–5.5 *Ma*), the less diverse ungulates would postdate the radiation recorded at Samos and precede the more pronounced decrease in carnivores and ungulates that occurred during the Pliocene. The absence of certain cosmopolitan species from Pikermi that occur at Samos and several other Eurasian and African localities could suggest a time difference. Similarly, certain Pikermi taxa that occur in several Eurasian

Table 11.—*Significant faunal differences between Pikermi and Samos—species which are abundant at one site and rare at the other.*

Species	Pikermi	Samos
Hipparion proboscideum	R	A
Hipparion dietrichi	R	A
Hipparion sp. (large, one preorbital fossa)	A	R
Hipparion matthewi	R	A
Sus major	A	R
Pliocervus pentelici	A	R
Helladotherium duvernoyi	A	R
Miotragocerus monacensis	A	R
Tragoportax spp.	R	A
Palaeoreas lindermayeri	A	R
Sporadotragus parvidens	R	A

A = Abundant (more than 30 specimens).
R = Rare (less than 30 specimens).

and African localities but not at Samos, again could be attributed to time.

In general there are no ancestral species at Pikermi with descendents at Samos. For most subfamilies Pikermi has fewer species than Samos except for Murinae, Mustelinae, Lutrinae, Hyaenidae subfamily D, Machairodontinae, and ?Giraffinae (Table 8). In the cases where the

Table 12.—*Significant faunal differences between Pikermi and Samos—presence and absence only of the abundant species.*

Pikermi	Samos
1. More birds	Less birds
2. *Mesopithecus pentelici*	—
3. —	*Thalassictis wongii*
4. —	*Orycteropus gaudryi*
5. *Chalicotherium goldfussi*	—
6. —	*Ancylotherium pentelicum*
7. —	*Chilotherium* four species
8. —	*Samotherium boissieri*
9. —	*Tragoportax rugosifrons*
10. —	*Prostrepsiceros houtumschindleri*
11. *Oioceros rothi*	—
12. —	*Criotherium argalioides*
13. —	*Protoryx laticeps*
14. —	*Protoryx crassicornis*

possibility of an ancestral species may exist, that species occurs at Samos also. Thus if time differences exist they probably are approximately plus or minus one million years.

Ecologic differences.—Table 11 shows species that are abundant at one locality but rare at the other. Table 12 shows the presence and absence of the abundant species. The differences indicated by these tables could be attributed to ecology. Presently, neither the general nor the degree of ecological differences between Pikermi and Samos are known. We have speculated elsewhere (Bernor et al., 1979) that the Mediterranean and northern China comprised a province characterized by the climaxing late Miocene sclerophyllous evergreen woodland. At the same time central Europe, the Siwaliks of India (Nagri and Dhok Pathan), and southern China were laurophyllous woodlands. In general there are more ungulates at Samos than at Pikermi. This may suggest minor ecological or seasonal differences. Presently it may be best to regard Pikermi and Samos as representing one or two relatively similar faunas (I am presently reconstructing the paleoecology).

Significance

Pikermi and Samos are exceptional localities. They contain species-rich faunas, which are concentrated in space and time. They are presently the best single time species-rich accumulations known and can be used as reference localities for biostratigraphy. The species-richness, the numbers of individuals, and the concentration of bone in space and stratigraphic thickness is of utmost importance for exploring further the rising possibility that the Samos species may represent communities close in space or perhaps one community. The quality of preservation is also exceptional and useful for systematics and paleobiology.

Summary and Conclusions

1. The Pikermi and Samos localities have been excavated for over 100 years. The brief history of the known expeditions is presented. The Samos quarries have been relocated.

2. Preliminary stratigraphic research indicates that most specimens were recovered in bone beds within overbank and paleosol sediments. At both Pikermi and Samos the bone beds are concentrated in space and time. At Samos all bone beds occur within the Mytilini Formation which could be considered to represent no more than 0.5 *Ma* of deposition. The age of the Samos fauna is 8.5–9 *Ma* only.

3. As a general rule, bone is well preserved indicating relatively minimal transport and relatively rapid burial. In addition, both localities represent species-rich faunas with many specimens. The origin of bone beds is not presently well understood. A tentative hypothesis proposes differential deposition of bones resulting in bone bed for-

mation; preferred accumulation and preservation in local depressions with bone destruction and removal from adjacent non depressed areas of the flood plains. Although other causes, such as droughts, are plausible causes for bone bed formation, it may not be necessary to hypothesize such catastrophies.

4. Reconstruction of species lists was accomplished with the help of many scientists and by identifying most specimens. Despite the number of previous studies, many unreported taxa almost doubled previous species lists. Revision of taxa shows the presence of many interesting species. Their systematic and paleobiologic study has just begun.

5. There are no major differences in stratigraphic level and in faunal content between the Samos bone beds. In general the faunal differences between Pikermi and Samos are small and attributable in part to sampling bias, time and ecology. The relative weight of each factor is not yet known. Presently, Pikermi and Samos are believed to represent one fauna or two relatively similar faunas. Samos has more ungulates and perhaps represents slightly more open habitat conditions than Pikermi or seasonal differences.

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